Reference: *Biol. Bull.* **163**: 197–210. (August, 1982)

PUMPING RATES AND PARTICLE RETENTION EFFICIENCIES OF THE LARVAL LAMPREY, AN UNUSUAL SUSPENSION FEEDER

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Abstract

The suspension feeding larvae of lampreys (ammocoetes) inhabit fine-grained sediments where particulate organic matter is concentrated, but whose low permeability limits the rate at which ammocoetes can pump water (flow rate). This study determined: 1) flow rates through the pharynges of ammocoetes, both within and out of the sediment, and 2) the ability of ammocoetes to filter particles from suspension (retention efficiency) over a wide range of algal cell concentrations (*Chlorella pyrenoidosa*, 1–75 mg/l).

For most suspension feeders, flow rate and retention efficiency must be measured indirectly (clearance method). Direct measurement was possible here, as ammocoetes remain apparently undisturbed in glass tubes that allow the separation of inhalent from exhalent ventilatory currents. Problems arise in attempting to use clearance methods to determine flow rates in burrowed suspension feeders, and these problems are discussed.

Ammocoete flow rates are exceptionally low compared to the rates of other suspension feeders, but retention efficiency was consistently high, even at the highest algal concentrations employed ($\bar{x}$ = 82%). While most suspension feeders rapidly process dilute suspensions, ammocoetes meet nutrient needs by slowly processing concentrated suspensions.

Introduction

Lampreys spend most of their life cycle as suspension feeding larvae (ammocoetes), living within the sediment of stream beds (Hardisty and Potter, 1971; Potter, 1980). Ammocoetes occupy burrows that are either open at one end (mouth) or are fully closed off from the overlying water. Suspended food particles are obtained from the water just above the substrate surface, and also from pore water within the sediment (Moore and Mallatt, 1980). Feeding involves trapping small particulate detritus and unicellular algae on mucus within the pharynx (Mallatt, 1979, 1981). Water is propelled by rhythmic muscular contractions of the pharyngeal wall, and by a pair of muscular flaps, the velum, at the anterior end of the pharynx (Rovainen and Schieber, 1975). Observations in this laboratory indicate ammocoetes extrude their exhalent water into the substrate around the burrow. Since the sediments occupied are fine sands and muds (see Fig. 1, and Malmqvist, 1980) of low permeability, ammocoetes must pump water against resistance. The thick, particle-trapping mucus, which fills most of the pharynx (Mallatt, 1981), also is likely to impede water flow.

Received 16 November 1981; accepted 18 May 1982.

Abbreviations: F, rate of water flow through pharynx; F′, clearance rate; RE, retention efficiency; W, wet weight of larvae.

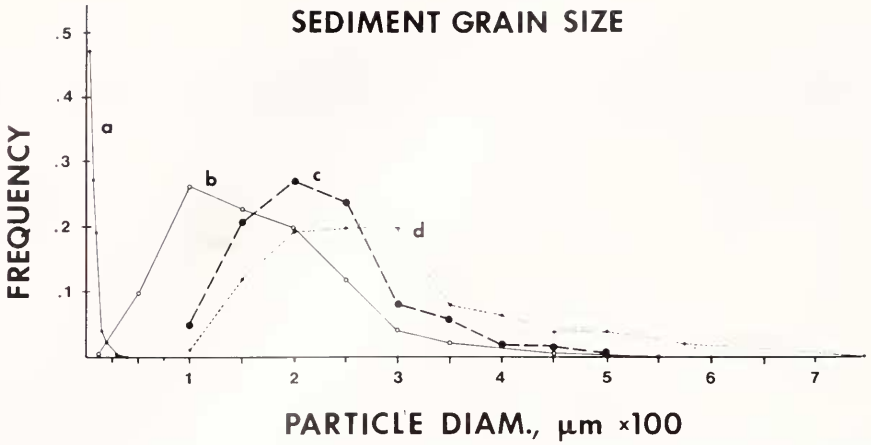

FIGURE 1. Size-frequency distributions of particles comprising several sediments in which ammocoetes will burrow and feed. That labelled 'a' is a diatomaceous earth, 'b' and 'c' are commercially obtained 70-mesh silica sands, and 'd' is a sand from an ammocoete habitat (*Petromyzon marinus*, Pere Marquette River, Michigan). Sand 'c' was used throughout this study. The numbers of grains measured exceeded 175 in all cases. As a measure of permeabilities, the times taken to drain 10 cm of water through 10 cm sediment columns are: a: 21 min; b: 6.5 min; c: 2 min; d: 2.75 min.

A search of the literature on suspension feeding animals (see especially Jørgensen, 1966, and Wallace and Merritt, 1980) revealed no other instance in which water is characteristically propelled into a fine-grained substrate. Most suspension feeders are either pelagic (crustacean zooplankton: Jørgensen, 1975; rotifers: Starkweather, 1980; frog tadpoles: Seale *et al.*, 1982), or if benthic, are epifaunal (bivalves: Winter, 1973; ascidian tunicates: Randløv and Riisgård, 1979). The infaunal suspension feeders that have been studied either inhabit coarse permeable sediment (amphioxus: Azariah, 1969; Webb, 1975) or have full access to the overlying water. Such access is achieved through U-shaped burrows (mayfly and midge larvae), siphons with inhalent and exhalent openings (infaunal bivalves), or protruding the filter into the overlying water (many polychaetes). In pumping against resistance, ammocoetes are unusual among suspension feeders. In fact, the existence of factors threatening to limit the rate at which ammocoetes can pump water seems to clash with the basic tenet of suspension feeding that large quantities of water must be processed rapidly (Jørgensen, 1975). How does such a suspension feeder survive?

Another unusual feature of ammocoete ecology is that the habitat contains comparatively high concentrations of suspended food particles. Due to natural processes of particle settling and resuspension, suspensions are expected to be more concentrated at the floor of a natural body of water than in the water column above (Hardisty and Potter, 1971). Supporting this, Moore (Moore and Potter, 1976, Fig. 1b; Moore and Mallatt, 1980, Fig. 1) measured higher levels of suspended organic solids at the substrate in ammocoete habitats (1–40 mg/l) than typically are present in open waters, where many other suspension feeders are found (below 1 mg/l; Jørgensen, 1975). The nature of their habitat suggests ammocoetes can efficiently process concentrated suspensions, and this merits experimental investigation.

With the special ecological features in mind, this work determines the rates at which ammocoetes pump water (flow rate) when in and out of sediment, and the

efficiency with which they remove food particles (retention efficiency) from suspensions of different concentrations.

Larval lampreys are ideal experimental animals for this type of study. For most other suspension feeders, flow rate and retention efficiency must be estimated indirectly, through monitoring the rates at which they clear particles from the water (clearance rates: see Jørgensen, 1975, for discussion). To utilize such a method, however, one must assume at some point that retention efficiency is 100%, an assumption that is untestable for most animals. For ammocoetes, flow rate and retention efficiency can be measured directly, as the larvae will feed in tubes, which allow separation of inhalent and exhalent currents.

This study provides some kinds of data seldom obtained for suspension feeders. Flow rates are measured in the absence of food particles, not possible with indirect methods. Also, this is one of the first studies in which retention efficiency is investigated as a function of particle concentration (also see Kurtak, 1978). In most past studies that have employed direct techniques on suspension feeders (Fiala-Médioni, 1978; Randløv and Riisgård, 1979), retention efficiency was related only to particle size.

Data on the flow rates of ammocoetes in glass tubes are supplemented by clearance rate data from burrowed individuals. Special problems arise in attempting to use indirect methods to determine the flow rates of burrowing suspension feeders *in situ*, and these are documented here.

Materials and Methods

This study primarily utilized larval *Petromyzon marinus*, which were obtained from the Muskegon and Pere Marquette rivers, Michigan, and from the Hammond Bay Biological Station, Millersburg, Michigan. A few Pacific lamprey ammocoetes (*Lampetra tridentatus*) were used, obtained from the Potlatch River near Bovill, Idaho. (Ammocoetes of different species are quite similar, morphologically and physiologically: Hardisty and Potter, 1971.) Stock animals fed on yeast and grew normally, averaging a 10% weight increase per month (Mallatt, unpublished). Experimental animals were between 10.1 and 11.1 cm long, with wet weights between 1.3 and 2.0 g ($\bar{x}$ = 1.6). All experiments were performed at 12°C.

The use of glass tubes to measure flow rate was inspired by Rovainen and Schieber (1975). Test chambers were glass pans (Fig. 2) divided into anterior and posterior compartments, holding 150 and 1100 ml of water, respectively. The water was dechlorinated tap water, previously filtered through a 0.45 μm Millipore® filter; water was continuously aerated in both compartments. The test animal occupied a glass tube, which pierced the partition. *P. marinus* larvae were employed whose pharynges fit snugly but without constriction into the tubes (0.6 cm internal diameter). Flow rates were monitored in dim light. Water pumped by the animal from the anterior compartment was replaced continuously, and the flow rate was considered to be the replacement rate (ml/hr, later adjusted for animal mass). Differences in water height between anterior and posterior chambers were kept low (<0.5 cm). It was determined, through removal and addition of known amounts of water, that the mean and maximum errors in the measure of flow rate were ±2 and ±5 ml/hr, respectively. In preliminary tests, dye (Methyl blue) added to the posterior compartment did not color water in the anterior compartment over an eight hour period with the ammocoete in place, so flow was unidirectional as expected.

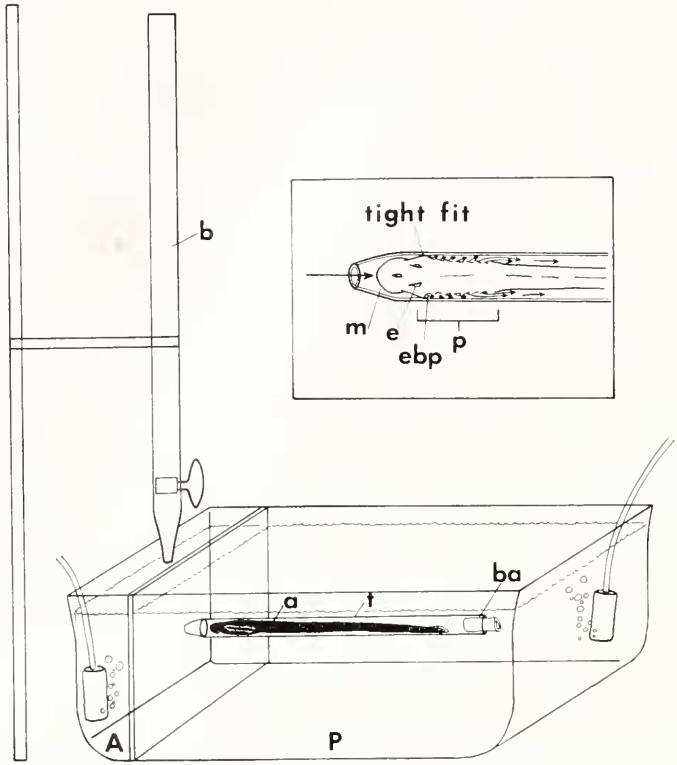

FIGURE 2. Apparatus employed for measuring: 1) flow rate through the pharynx, and 2) particle retention efficiency, of larval *P. marinus*. Ammocoete (a) in the tube (t) pumps water from the anterior compartment (A) to the posterior compartment (P). Inset shows tube in dorsal view. Other symbols: b, buret; ba, balloon attachment site; e, eye; ebp, external branchiopores; m, mouth; p, pharynx.

The experimental procedure involved monitoring the flow rates of 12 individual ammocoetes for periods of 4 to 13 hours, after an 18 hour period of adjustment to the apparatus. The reason flows were monitored over time was to determine whether the confinement of the tubes stressed the ammocoetes, as might be reflected in a cumulative tendency to increase or decrease flow rate (Cairns *et al.*, 1982).

For measuring the clearance rates of buried ammocoetes, an indirect technique was used, similar to that of Malmqvist and Brönmark (1982). The test chambers were five-liter aquaria, containing four liters of continuously aerated, dechlorinated tap water, one liter of which occupied the interstices in two liters of a silica sand (Fig. 1, sand 'c'). Two test aquaria were employed, one containing *P. marinus*, and the other, *L. tridentatus* ammocoetes (four to six per tank, 8–12 g). Each test tank was paired with a control tank that lacked ammocoetes.

This test of clearance rates lasted two months, with trials conducted daily. At the onset of each trial, fresh yeast suspension (*Saccharomyces cerevisiae*, Fleischmann's® cakes) was added to the water above the sediment of test and control tanks, in amounts that varied randomly from trial to trial, to yield particle concentrations ranging from 5 to 2700 mg (dry) per liter. Yeast cell concentrations in the water above the sand (C) were measured visually with a hemocytometer at the onset (C_1) and the end (C_2) of the four to eight hour duration (T) of each

trial. The rates at which burrowed ammocoetes cleared particles from the overlying water (F', ml/g/h) were calculated according to the equation:

$$\text{Clearance Rate} = F' = \frac{3000 \text{ ml } [(\ln C_{1,t} - \ln C_{2,t}) - (\ln C_{1,c} - \ln C_{2,c})]}{T \cdot W}$$

where 3000 ml is the volume of overlying water, W is the wet weight of the larvae in the test tank, and the subscripts t and c denote test and control tanks, respectively (Coughlan, 1969). The water was changed and the sand was washed after each trial. Trials were conducted in the dark. Variation in cell settling rates in control *versus* test tanks led to the occasional calculation of negative clearance values; these were treated as zero (or as one ml/g/h for log-transformed data).

Another experiment was performed to relate flow rates measured for ammocoetes in tubes to the clearance rates of burrowed individuals. Here, the effect of the sand's resistance on flow rate was tested directly. Three *P. marinus* larvae that had been used in clearance studies were placed in the tube devices. A flexible plastic tube was then fit snugly around the posterior end of each glass tube, and the rate at which the ammocoete propelled water through the plastic tubing was monitored before and after the insertion of a plug of sand. The latter was 4 cm long, approximating the depth at which many buried ammocoetes resided in stock tanks. The plastic tube was bent slightly to assure the sand entirely filled the width of its lumen.

Several things should be noted about the construction of Table I, where flow rates are compared among many groups of suspension feeders. These figures can

TABLE I

Flow rate in different suspension feeders

Animal	Wet weight (g)	Flow rate (ml/g/h)	Flow rate adjusted to 1.6 g wet body mass[a]
1. Copepods			
a. *Calanus helgolandicus*	1.2×10^{-3}	15,800	2,600
b. *Calanus pacificus*	1×10^{-3}	7,600	1,200
2. Lamellibranches			
a. Various bivalves[b] (13 species)	1.6	600–5000 $\bar{x} = 1600$	600–5000 $\bar{x} = 1600$
b. *Crassostrea virginica*	1.0	1,580	1,560
c. *Pecten irradians*	3	1,000	1,170
d. *Mytilus edulis*	1.6	190–625	190–625
e. Various bivalves[b] (3 species)	1.6	125–625	125–625
f. *Dreissena polymorpha*	5×10^{-1}	150	110
3. Cladocerans			
a. *Daphnia pulex*	2.2×10^{-5}	3,400	370
b. *Daphnia magna*	5.0×10^{-5}	4,000	530
4. Rotifers			
a. *Keratella cochlearis* (large)	3.7×10^{-7}[c]	21,600	470
b. *Keratella cochlearis* (small)	1×10^{-7}	25,000	400
c. *Conochilus dossuarius*	6×10^{-7}	9,700	240
d. *Kellicottia bostoniensis*	3.7×10^{-7}	2,300	50
5. Sponges			
a. *Sycon coronatum*	1.25	980	920
b. *Halichondria panica*	3.0	370	430

TABLE I—(*Continued*)

Animal	Wet weight (g)	Flow rate (ml/g/h)	Flow rate adjusted to 1.6 g wet body mass[a]
6. Bryozoan			
Zoobotryon verticillatum	5.5×10^{-5}	6,700	290
7. Ciliates			
a. Algavores (large cells) *e.g.*,			
Stylonychia mytilius	5×10^{-8}	500,000	1,300
b. Feeders on intermediate-sized cells (2–5 μm diam) *e.g.*,			
Paramecium	2.5×10^{-8}	24,000	270
c. Bacterivores *e.g.*,			
Tetrahymena pyriformes	1×10^{-8}	5,000	45
8. Infaunal Polychaetes, and other burrowing worms			
a. Sabellidae			
Myxicola infundibulum	2.7	100	115
Schizobranchia insignis	1.0	70	60
Sabella pavonina	1.9×10^{-1}	390	230
b. Serpulidae			
Potamoceras triqueter	1.9×10^{-2}	1,400	460
Hydroides norvegica	1.2×10^{-2}	900	260
Spirorbis borealis	2×10^{-4}	950	100
Salmacina dysteri	1×10^{-4}	2,090	190
c. *Chaetopterus variopedantus*	6	50	70
d. *Urechis caupo* (Echiuroidea)	21	900	1,230
9. Chordates			
a. Various tunicates (7 genera)	1.6	95–560, $\bar{x} = 225$	95–560, $\bar{x} = 225$
b. *Branchiostoma lanceolatum*	1.5×10^{-2}	200–316	70–100
c. *Hyla crucifer* (frog tadpole)	0.2	25–65	15–40
d. *Bufo woodhousei* (frog tadpole)	0.15	50–140	30–80
e. Larval *Petromyzon marinus*	1.6		8–64, $\bar{x} = 28$ (in tube)

SOURCES: 1a. Paffenhöfer (1976), Fig. 3; 1b. Runge (1980), Table 3 (September value); 2a. Møhlenberg and Riisgård (1979); 2b. Palmer (1980), Table III; 2c. Jørgensen (1966); Fig. 1.40; 2d,e. Foster-Smith (1975), Figs. 1,2; 2f. Walz, (1978), Fig. 2; 3a. Crowley (1973); 3b. Ryther (1954), Figs. 2,4; 4. Bogdan *et al.* (1980), p. 74–75; 5a,b. Foster-Smith (1976), Table IV; 6. Bullivant (1968); 7. Fenchel (1980a), p. 18 and Fig. 4; 8. Jørgensen (1966), Table 1.1 and p. 11; 9a. Randløv and Riisgård (1979), Fig. 4; 9b. Azariah (1969); 9c,d. Seale and Beckvar (1980); 9e. present study.

NOTE: Essential data on food type and experimental temperature are as follows: 1a. Various algae at a range of concentrations, 15°C; 2a. Various unicellular algae, 2 to 10×10^4 cells/ml, 10–13°C; 2b. *Thalassiosira, Isochrysis* and *Dunaliella*, 21°C; 2c. "Flagellates and diatoms", 22–26°C; 2d,e. No information given; 2f. *Nitschia actinastroides*, 0–24 mg/l, 15°C; 3a,b. *Rhodotorula* sp., 20°C; 4a,c,d. *Chlamydomonas*, 20°C; 4b. *Rhodotorula*. 20°C; 5a,b. No information given; 6. *Monochrysis*, 24°C; 7. See legend to Fenchel's (1980a) Fig. 4; 8a–c. Colloidal graphite particles, 16–20°C; 8d. Direct measurement, 20°C; 9a. See legend to Fig. 4 in Randløv and Riisgård (1979); 9b. "Normal sea water", 29°C; 9c,d. *Anabaena sphaerica*, 0.2–20 mg/l, 21°C; 9e. Unfed, or fed on *Saccharomyces cerevisiae*, 12.5°C.

[a] Assumes $F \propto W^{0.75}$: See Materials and Methods section. Values also assume animals' dry weights are 20% of wet weight.

[b] See Winter (1973, 1978) and Foster-Smith (1976) for more data on flow rates in bivalves.

[c] Rotifer weights calculated from body lengths assuming $W \propto L^3$ between genera.

be compared only broadly, as measurements reported in the literature were obtained by different methods and at different temperatures (but mostly between 12 and 22°C). An attempt was made to correct for the most important source of variation in published values of flow per body mass (F/W), the effect of animal size. This was done through assuming $F \alpha W^{0.75}$, *i.e.*, $F/W \alpha W^{-0.25}$. Studies on a variety of suspension feeders support this assumption (Azariah, 1969; Paffenhöfer, 1971; Jørgensen, 1975; Møhlenberg and Riisgård, 1979; Fenchel, 1980a; Palmer, 1980), and Winter (1978) discussed it at length. In constructing the table, it was also necessary to assume dry weights of the animals were 20% of wet weight.

Retention of *Chlorella pyrenoidosa* cells was measured for *P. marinus* ammocoetes. The algae (diameter: $\bar{x} = 8.7 \pm 2.0$ μm S.D.) were grown in High Salt Medium (Sueoka, 1960), then washed via centrifugation and resuspension in filtered tap water. Control experiments indicated algal numbers did not measurably increase during experimental periods, presumedly because of low light levels. Percent efficiency of particle retention was assessed by two techniques. In both, algae were added to the anterior chamber of the tube device. In the first technique, the algal concentration was held constant for an interval during which a deflated balloon, fitted around the posterior end of the tube, collected the exhalent water. The balloon was never allowed to fill to the level where it exerted back pressure on the larva. Samples were removed from the balloon and the anterior compartment, diluted 4:1 with 0.1% NaCl, and their particles were counted six times with a Model FN Coulter Counter. Retention efficiency was calculated as:

$$RE = 1 - \frac{C_b}{C_a}$$

where C_b and C_a are the numbers of algae counted per ml from the balloon and anterior compartment samples, respectively.

In the second technique, no balloon was used. Here, the algal concentration in the anterior compartment decreased as the volume pumped from it by the ammocoete was replaced experimentally with clean water. Retention efficiency was calculated by the equation:

$$RE = \frac{C_{fp}V_{fp} - C_{ip}V_{ip}}{C_{ia}V_{ia} - C_{fa}V_{fa}}$$

where C_{ia} and C_{fa} are initial and final particle concentrations respectively in the anterior compartment, C_{ip} and C_{fp} are initial and final particle concentrations respectively in the posterior compartment, V_{ia} and V_{fa} are initial and final volumes of suspension respectively in the anterior compartment, and V_{ip} and V_{fp} are initial and final volumes in the posterior compartment. Again, particle concentrations were measured with the Coulter Counter.

Retention efficiency was calculated a total of 22 times, based on 7 individuals, for algal concentrations ranging from 1 to 75 mg (dry) per liter.

Results

Ammocoetes in the tubes usually remained still, wiggling ("crawling", Rovainen and Schieber, 1975) being infrequent. All the individuals exposed to *Chlorella* produced green feces about six hours after the presentation of food. Ammocoetes dug from the sand following exposure to yeast contained white cords within their guts, visible through the ventral skin. These findings suggest the larvae fed normally under experimental conditions. Burrows and tubes were never lined by mucus (*cf.* Sterba, 1953).

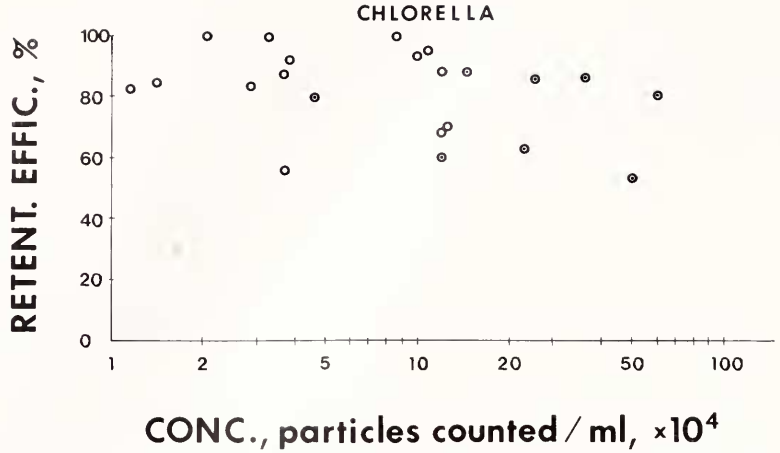

FIGURE 3. Percentages of *Chlorella pyrenoidosa* cells retained by larval *P. marinus* over a range of cell concentrations. Data pooled from seven ammocoetes. A count of 2.25×10^5 particles/ml corresponded to 27 mg dry mass per liter. The open dots represent values measured by collecting pharyngeal efflux in a balloon, while the closed dots were obtained by the dilution method described in the text. The least squares equation (linear) for all the points is:

$$RE = 86 - 2.94 \times 10^{-6}\ C, \qquad r = -0.33, \qquad P > 0.10.$$

Retention efficiency data are depicted in Figure 3. For concentrations of *Chlorella* between 1 and 75 mg/l, the fraction of particles removed was high, averaging 86 ± 13% S.D. and 75 ± 13% S.D. respectively, as measured by the balloon and dilution techniques. These means did not differ statistically from one another at the 95% confidence level ($t = 1.96$, $P > 0.05$), so the overall retention efficiency was calculated as 82 ± 14% S.D. There was no evidence that retention efficiency varied with algal concentration in the range studied.

Flow rates recorded for ammocoetes in the tubes are shown in Figure 4. One hundred and one hourly recordings, compiled from twelve individuals, ranged from 8 to 64 ml/g/h. The overall average hourly flow rate was 28 ml/g/h, with a standard deviation of 13. Individual average flow rates during the monitoring periods ranged from 10 to 52 ml/g/h in the twelve animals. Did flow rate tend to change with the amount of time spent in the tube? When both increases and decreases are considered, the mean hourly change did not differ significantly from zero (+3.2% ± 28% S.D., $P > 0.3$). Absolute hourly changes averaged 22%. Thus, although flow rates varied considerably over time, no consistent pattern of variation was evident.

Clearance rates recorded for burrowed ammocoetes are depicted in Figure 5. The quite similar results from the two species were combined. Mean clearance rates ranged from 3 to 13 ml/g/h, depending on the concentration of yeast in the overlying water, with an overall average of about 7 ml/g/h.

The placement of a 4-cm sand plug in the path of pharyngeal efflux of three ammocoetes in tubes led to decreases in flow over previous rates. Declines averaged about 50% (30 to 11, 23 to 15, and 19 to 11 ml/g/h).

DISCUSSION

It could be suggested that confining ammocoetes within tubes affected flow rate, either physically—the glass walls interfering with movement of water out of the

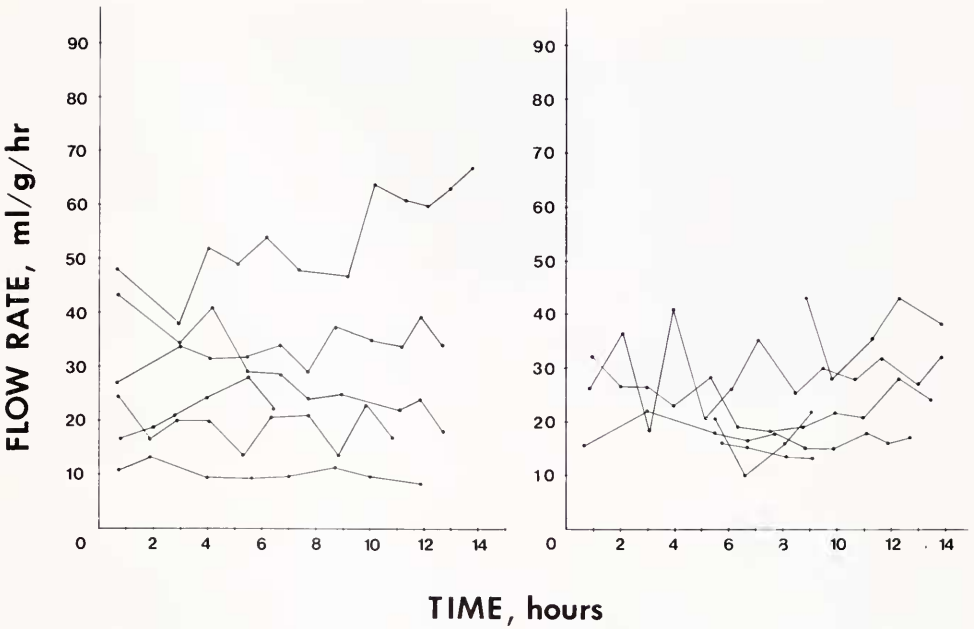

FIGURE 4. Variation in flow rate over time in twelve nonfeeding *P. marinus* larvae ($\bar{x}$ = 1.6 g), each within the device of Figure 2, at 12°C. Two graphs are used to avoid crowding. No consistent pattern of change is evident.

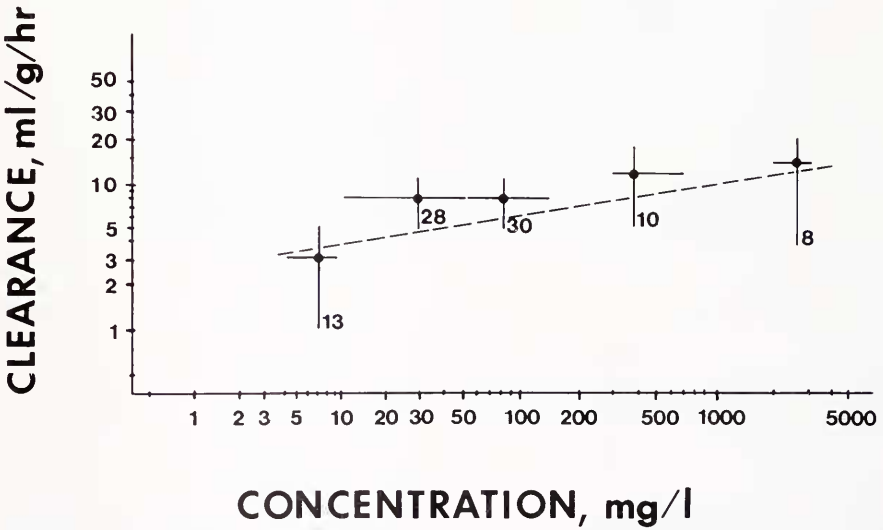

FIGURE 5. Response to yeast cells (*Saccharomyces cerevisiase*) of ammocoetes ($\bar{x}$ = 2.0 g) burrowed in sand, particle clearance rate vs. food concentration in the overlying water. Data from two species *P. marinus* and *L. tridentatus* were very similar (analysis of covariance, $P > 0.25$ for both slopes and intercepts of the log-transformed lines), and are combined. The least squares equations, calculated from the log-transformed data, are: for *Petromyzon*, $F = 2.9 \cdot C^{0.17}$ (46 points, $r = 0.29$, $P = 0.05$); for *Lampetra*, $F = 2.3 \cdot C^{0.25}$ (43 points, $r = 0.37$, $P < 0.05$); and for the combined data, as graphed, $F = 2.3 \cdot C^{0.21}$ ($r = 0.33$, $P < 0.01$). The dots represent mean values for points in the concentration ranges indicated by the horizontal bars. Vertical bars delineate 95% confidence intervals for clearance rates, and the numbers of points used in calculating these intervals are indicated below these bars. At 12°C.

gill pores—or behaviorally, through stressing the animals. Speaking against physical interference, it is noted that flow from the gill pores is normally posterior, not lateral (unpublished observations, on free animals presented concentrated carmine particle suspensions.). Speaking against stress, it is noted that larvae in tubes efficiently ingested food (Fig. 3), and seldom exhibited crawling behavior. The lack of any direction of variation in flow rate with time (Fig. 4) is also consistent with the view that the ammocoetes were not stressed. Indeed, placement in a tube seems to calm this burrowing organism (thigmokinesis: Hardisty, 1979, p. 56; the calming effect was also noted by Rovainen and Schieber, 1975).

Rovainen and Schieber (1975) validly point out that such tubes may interfere with cutaneous respiration, leading to a compensatory elevation of flow through the pharynx. The degree to which ammocoetes rely on cutaneous respiration is unknown (Lewis, 1980), although the thickness of the dermis suggests that the gills are much more important respiratory structures than the skin (Czopek and Sawa, 1971). Furthermore, opportunity for cutaneous respiration should be curtailed when ammocoetes occupy poorly permeable substrate. An overestimate of flow rates would not affect the conclusions of this paper.

The test of retention efficiency employed here measured the fraction of particles removed from suspension, not the fraction that actually entered the gut. It is conceivable that some error was introduced through the ammocoetes rejecting particles after filtration, or by some cells settling within the tubes and never reaching the balloon (although nothing was seen that indicated these things occurred). In future studies, the methodology will be expanded to include a quantification of gut contents.

Malmqvist and Brönmark (1982) determined clearance rates of *Lampetra planeri* ammocoetes in sand. Using the same technique, I obtained average clearance rates (7 ml/g/h) that are comparable to theirs (11 ml/g/h), considering that their animals were smaller (0.6, *cf.* 1.6 g) and the temperature, higher (15°C). However, those authors apparently considered their clearance rates to reflect flow rates, which may not be correct. In the technique employed, a mass of clean water, within the pore space of the sediment, is interposed between the ammocoetes and the overlying suspension. To the extent that the ammocoetes use this clean water, particles will not be cleared, and clearance rates will underestimate flow rates. That the discrepancy is significant is indicated by the observation that most ammocoetes in the test aquaria had closed burrows, cut off from the suspension overhead. As the flow rates of the burrowed ammocoetes in this study cannot be measured by clearance rates, they must be estimated by simulation. When pumping against a sand plug, whose length approximated the depth at which burrowed ammocoetes reside, larvae in tubes moved water at about half their unimpeded rate; thus, flow rates for the burrowed animals in this study are estimated as half those of unburrowed individuals, or about 15 ml/g/h.

In this study, ammocoetes filtered most ($\bar{x} = 82\%$) *Chlorella* particles from suspension over a range of concentrations, 1–75 mg/l, that should include those they experience in nature. Many suspension feeders begin to perform inefficiently when concentrations exceed 1–10 mg/l, rejecting particles (Jørgensen, 1975, pp. 64–65; Epifanio and Ewart, 1977). The evidence for efficient retention by ammocoetes at concentrations as high as 75 mg/l supports the hypothesis, proposed in the Introduction, that lamprey larvae are adapted to filter concentrated suspensions. The extensive system of feeding mucus may allow this.

Average flow rates, as measured for the animals in tubes, varied among individuals by a factor of five (10–52 ml/g/h). This large variation is noteworthy,

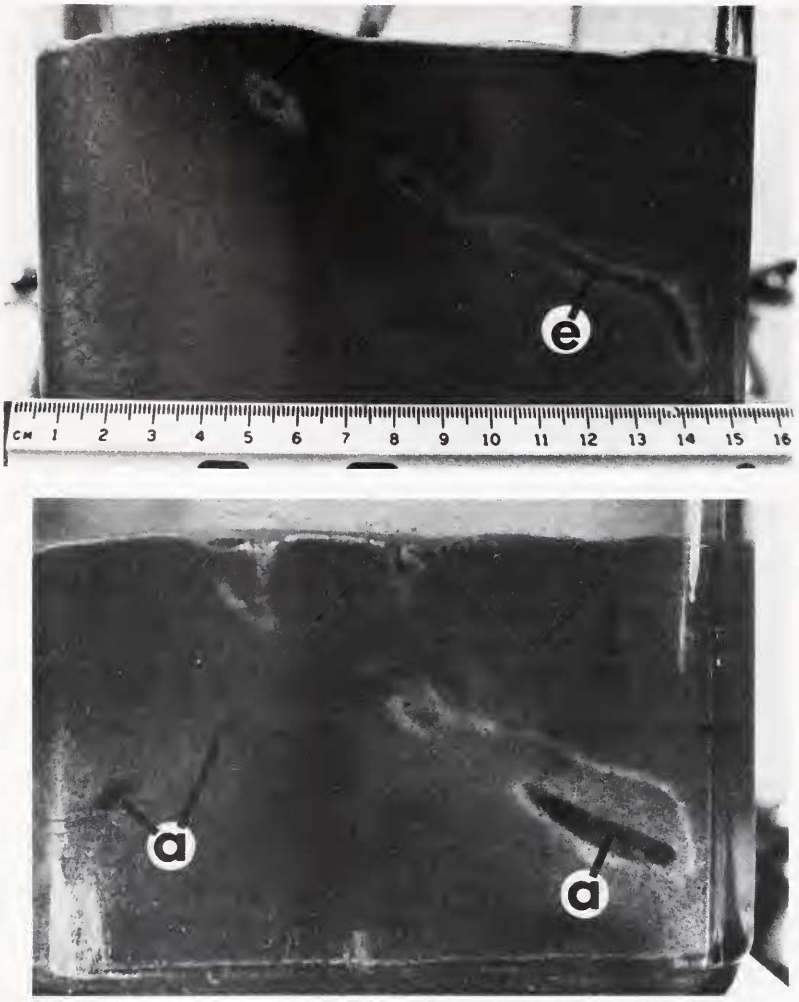

FIGURE 6. Photographs demonstrating that ammocoetes propel exhalent ventilatory water into the surrounding sediment. Above is shown an empty burrow (e) against the wall of an aquarium; below are two burrows containing ammocoetes (a). Most of the sand is dark, containing reduced organic matter. Above, a thin rim of light, oxidized sand outlines the empty burrow. This demonstrates the low permeability of the sand, aerated water having only diffused a few mm into it. Below, both ammocoetes (a) are surrounded by light halos, 1–2 cm thick, produced by their pharyngeal efflux. Such halos also surrounded ammocoetes buried in a very fine grained diatomaceous earth, although the light zones were thinner there. Oxidized zones also have been noted around infaunal deposit feeders (Aller, 1978, Fig. 1).

considering animal weights, temperature, and treatments were all standardized. Rovainen and Schieber (1975, their Table 1) also recorded large individual variation in flow rates; these ranged from 20 to 60 ml/g/h for undisturbed ammocoetes at 20° weighing 0.85–2.7 g.

In the present study, flow rates were calculated to average 28 and about 15 ml/g/h for unburrowed and burrowed ammocoetes ($\bar{x}$ = 1.6 g, 12°). Preliminary results from similar animals in tubes indicate that the presence of food (yeast) can increase flow rate by up to 50%, to about 50 ml/g/h (Mallatt, 1980). Even so,

ammocoete flow rates are probably the lowest ever recorded for a suspension feeding animal, even when adjusted to compensate for the ammocoete's comparatively large size (Table I, fourth column). The low flow rates of ammocoetes are more like those produced by animals that do not depend on suspension feeding, such as macrophagous fish (Randall, 1970), infaunal deposit feeders (*Echinocardium* and *Malacoceras*: Foster-Smith, 1978), and some facultative suspension feeders (*Arenicola* and *Bithynia*: Jørgensen, 1966).

Several factors could be responsible for the low rate at which ammocoetes pump water. Most obviously, this should relate to the resistance of the substrate inhabited, which would preclude the evolution of a rapid flow rate. The quantity of intrapharyngeal mucus might also limit ammocoete flow rate, as do the fine mesh filters of some holotrich ciliates (Fenchel, 1980a,b).

This analysis reveals two peculiarities of ammocoete feeding. Compared to other suspension feeders, ammocoetes 1) pump water extremely slowly, and 2) are able to filter very concentrated suspensions. These are interrelated. Slow flow *allows* concentrated suspensions to be utilized in that, by presenting little food-carrying water to the filtering surfaces per unit time, it diminishes the tendency of these to saturate. Low flow rate also *demands* high food concentration, for only concentrated suspensions could be expected to fill nutrient needs when little food-carrying water is available per unit time.

An hypothesis of the ammocoete feeding strategy emerges from this analysis. Whereas most suspension feeders meet their food requirement by moving dilute suspensions rapidly across their feeding structures, ammocoetes cannot grow on dilute suspensions. A slow rate of water flow through the pharynx, necessitated by the high resistance of the substrate inhabited and the design of the pharyngeal pump, confines ammocoetes to environments where food suspensions are concentrated. Since the burrowing habit that limits flow rate is necessary for protecting lampreys from predation during the larval stage (Morman *et al.*, 1980), the requirement for concentrated suspensions seems basic to the animal's biology.

The peculiarities of ammocoete feeding could be of general ecological interest. The ability of infaunal animals to modify the chemistry of the substrate they inhabit has recently received much attention (Aller, 1980; Gust and Harrison, 1981; Lawrence *et al.*, 1982). For ammocoetes, which drive the overlying water directly into the sediment (Fig. 6), habitat modification could be considerable.

Acknowledgments

This work was partly supported by the Basic Medical Sciences Program (WAMI) at Washington State University; part was performed at the University of Chicago, Dept. of Anatomy, under the support of the University's Hinds and Nierman Funds. I would like to thank Kwen-Scheng Chiang, J. J. Gilpin, James Huber, Timothy Holtsford, Aniko Juhasz, Natasha Matkin, David Swinton, Richard Wallace, and Richard Wassersug for help with various aspects of this study. Martin Feder, Bruce Frost, Karin Hoff, G. R. Harbison, Mike LaBarbera, J. T. Lehman, Richard Parker, Dianne Seale, and Richard Wassersug critically read various versions of the manuscript.

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